

- Stresemann, E. & Stresemann, V. 1972. Über die Mauser in der Gruppe *Lanius isabellinus*. *J. Orn.* 113: 60–75.
- Vaurie, C. 1959. *Birds of the Palearctic fauna*. Passeriformes. H. F. & G. Witherby, London.
- Voous, K. 1960. *Atlas of European birds*. Nelson, London.

Address: D. J. Pearson, 4 Lupin Close, Reydon, Southwold, Suffolk IP18 6NW, U.K.

© British Ornithologists' Club 2000

## A new montane subspecies of *Sheppardia gunningi* (East-coast Akalat) from Tanzania

by J. Fjeldså, M. S. Roy & J. Kiure

Received 9 September 1998

The Nguu (Nguru North) Mountains in Tanzania constitute a very steep montane area, which is part of the famous Eastern Arc Mountains but rather isolated at the edge of the dry Maasai steppe. The first ornithological survey of these mountains was conducted by the 'Project Mount Nilo '95 Expedition' from the University of Cambridge, U.K. (Seddon *et al.* 1995). Among the interesting discoveries was a population of akalats, identified as *Sheppardia gunningi*, East-coast Akalat. Many birds were mist-netted and photographed, and a good description was provided in the trip report, but no specimens were collected.

Some concerns about the identity of these birds might exist because of the similarity of akalats species (at least in certain field guide illustrations) and because other Tanzanian montane forests are occupied by *S. sharpei*, Sharpe's Akalat (while *S. gunningi* inhabits coastal forests below 300 m in Tanzania). In order to settle the identity of this population, Jacob Kiure visited the Nguu Mts again 13–29 November 1996, and collected a series of specimens which are now kept in the Zoological Museum, Copenhagen (ZMUC). The Nguu population clearly represents *S. gunningi*, but differs from adjacent coastal populations, morphologically and genetically. We will describe it here as a separate subspecies, which we name.

### *Sheppardia gunningi alticola* ssp. nov.

*Holotype*. ZMUC kat.nr. 92.216, adult male, 27 November 1996, Lulago Forest in Nguu Mts (5°34'S, 37°28'W).

*Paratypes*. ZMUC kat.nr. 92-217-29, collected in the Nguu Mountains by J. Kiure, in Gombero Forest 13–25 November and Lulago Forests 27–29 November. Also tissue samples of all specimens are deposited in the ZMUC.

*Etymology*. The subspecific name emphasises its isolated occurrence in a high-altitude habitat island.

*Description of the holotype.* Capitalised colours refer to Ridgway (1912). Upperparts from forehead to rump olive-brown (ranging from Mummy Brown on top of head to Dresden Brown back, with buffy white subapical spot on lower rump feathers), upper tail Deep Quaker Drab with olive-brown outer edge basally. Lower forehead, lores and lower orbital area Dark Quaker Drab, separated by semi-concealed and faint whitish stripe from Deep Neutral Grey upper lore, superciliary and upper posterior orbital area; cheeks and ear-coverts greyish olive-brown. Upper wing-coverts Neutral Grey, greater coverts with olive-brown outer edge; remiges Deep Neutral Grey with olive-brown outer webs on tertials and secondaries, light grey on primaries; inner webs creamy white, broadest on tertials and secondaries. Underparts from chin to under tail coverts and axillaries Yellow-ocher/Deep Chrome, with white basal parts of feathers shining through on chin and upper throat, belly Light Orange-Yellow, white centrally; upper flanks washed olive-brown; under wing coverts dark greys broadly tipped white. Bare parts: bill uniform dark brown; iris dark reddish-brown; legs pink-grey, soles yellow. Measurements (mm): wing 72.2 (method 2 of Svensson 1992), 5th fully developed primary (in descending order) longest, exceeding 4th-1st by 1.3, 5.6, 16.2 and 34 mm, respectively; culmen 12.6; tarsus 21.8; tail 55.

*Diagnosis.* Differs from *S.g. sokokensis* of the adjacent coastal zone by large size, distinctly darker grey face, more chrome-yellow underparts with restricted white on belly. Large size and restricted extension of white on the belly approaching *S. g. beusoui* from Malawi which, however, has a more prominent white loreal stripe and a warmer general colouration.

*Individual variation.* Seddon *et al.* (1995) provided a general description based on 21 mist-netted birds, which suggests no individual variation in plumage colours. Weights were 14.5–20.0, average 17.3 g (measurements given for these live birds are not useful for comparison with museum specimens). We examined 13 collected specimens, 10 adult, 1 immature and 2 fledglings. Adults were constant in appearance, some specimens slightly more buffy citrine on lower back. The immature was lighter overall, with tips of greater wing-coverts and narrow edges of tertials cinnamon-buff. Fledglings were Clove Brown above, each feather with large Cinnamon-Buffer spot centred on feather shafts and especially the greater wing coverts margined black; below buffy, to white on belly, with feathers of throat, breast and sides edged Fuscous. Wings of 5 adult males (incl. type) 70.0–75.0 (average 73.0), six females 68.0–72.2 (average 69.7).

*Distribution.* *Sheppardia gnuuungi alticola* is evidently endemic to the Nguu Mountains in northwestern Tanga, Tanzania (5°27–38'S, 37°26–36'E). Here, forest exists from 850 to 1,750 m, as four main fragments and some small fragments on lower hills nearby, with altogether 140 km<sup>2</sup> forest cover (1:250,000 Land Cover Maps of Tanzania, based on satellite imagery from 1994–6).

### Comparison with other akalats

Notes on akalat specimens have been taken during several museum visits: The American Museum of Natural History (New York), Kenya National Museums (Nairobi), The Marshall Field Museum (Chicago), The Natural History Museum (Tring) and the Milwaukee Museum. Specimens were borrowed in 1998 for direct comparison with Nguu specimens from The Natural History Museum. The subspecies variation is reviewed in Benson (1947) and Keith *et al.* (1992). *S. g. sokokensis* (coastal forests of Kenya and Tanzania, from lower Tana River to Rondo area) varies from Buff-Yellow to a rich Yellow-ochre on the breast, with extensive white belly and buff vent (the pale-breasted birds being immatures), and lores and supercilium are brighter bluish grey than *alticola* (Benson 1947). It is small (wing of 11 males 67–72, average 70.5, 7 females 63–72, average 65.6). *S. g. bensoni* (Malawi) is much more richly coloured, Cinnamon-brown to Dresden Brown above and uniform Ochraceous-orange below, from chin to vent, except for a lighter Ochraceous-buff lower belly with a small white central stripe. It resembles *alticola* in the restricted extension of white on the belly and by its large size (wing of 8 males 72–78, average 74.8, 3 females 68–70, average 69.0), but differs clearly in having a more conspicuous white loreal stripe and a general colouration much more like *S. cyornithopsis* and *aequatorialis*, Common and Equatorial Akalats. *S. g. gunningi* (Mozambique lowlands) has restricted dull grey lores and supercilium, and is rather dull coloured overall (almost as *S. sharpei*), Snuff Brown above and rather brownish orange (Ochraceous-Tawny to Cinnamon Buff) on the breast, and with extensively white belly and Light Buff vent; size small (wing of 13 males 72–76, average 74.1, 4 females 65–68, average 67.2). Weights (in g) for *S. g. gunningi* are 17–20, average 18, for 8 males; 16–17, average 16.7 for 3 females; for *S. g. sokokensis* 13 and 17 for two males and 12–15.3, average 14.1 for 7 females (Keith *et al.* 1992).

### Molecular data

Differentiation at the DNA level was studied as part of a broader evolutionary study of akalats (unpublished). We report here only on those data which are relevant for evaluating the systematic relationships of *S. gunningi*.

Blood and feathers sampled from the field were stored in a DMSO/NaCl solution (Seutin *et al.* 1991). Two samples per site were used. DNA extraction and amplification followed standard protocols for single stranded template Dideoxy sequencing. Sequence data were compared from two mitochondrial DNA (mtDNA) genes, namely 302 base pairs of the Cyt b gene (amplified using the primer pair L15546 and H15915; Edwards *et al.* 1991) and 308 base pairs of the mtDNA ND2 gene (using primers H5578 and L5215; Hackett 1996). Sequences were aligned visually using the program SeqApp (Gilbert 1992), and aligned sequences were analysed using parsimony for phylogenetic reconstruction (PAUP vers. 3.1.1, Swofford 1991) and bootstrap analysis (Felsenstein 1985). Gene sequences were combined into a total evidence data set.

Fig. 1 shows the most parsimonious tree of 200 steps. There is full bootstrap support for a sistergroup relationship between *S. gunningi* and *S. sharpei*, with all members of each species placed together, and an average sequence divergence of

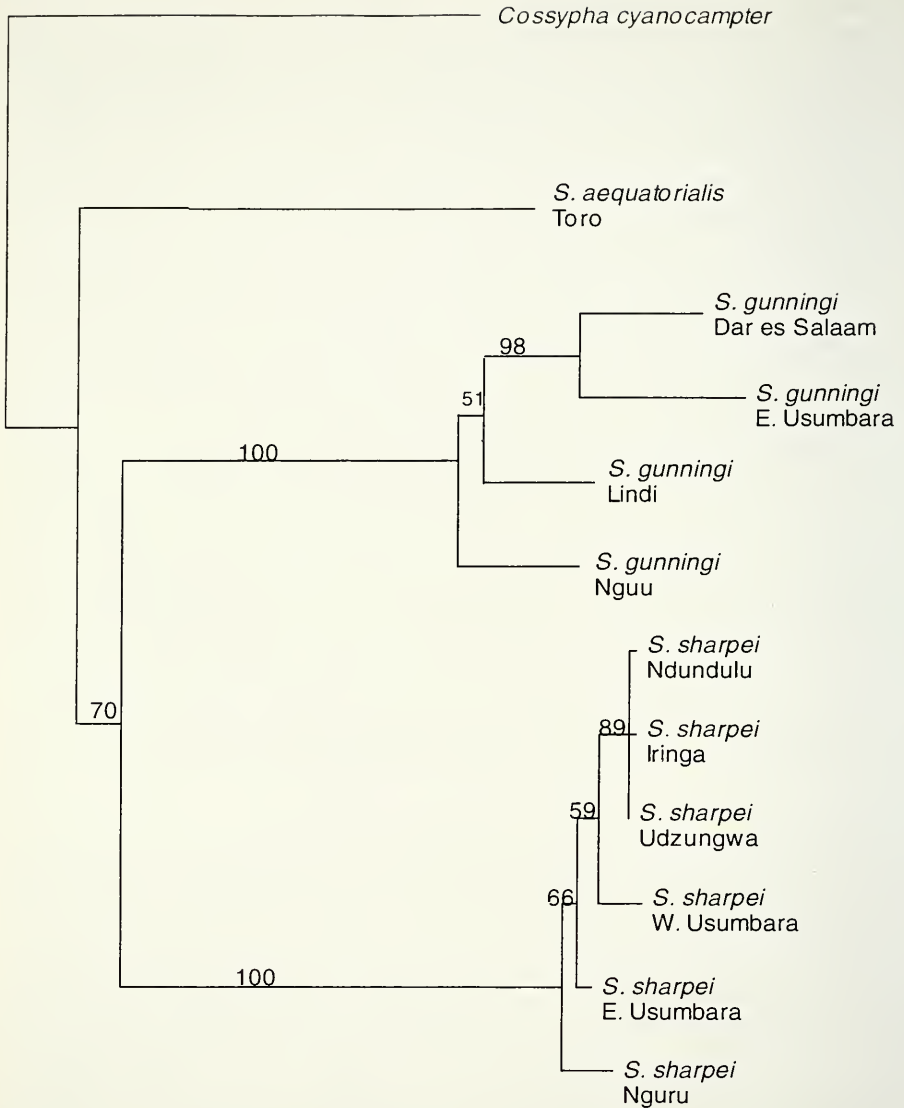


Figure 1. Phylogeny of three closely related akalats of eastern Africa, based on two mtDNA gene fragments of altogether 611 bp. Parsimony analysis with 3rd position transversions weighed 10 times transitions; figures give per cent support from >500 bootstrap replicates. *S. cyornithopsis* (not shown) clusters closely together with *aequatorialis*, and these two could well prove to be conspecific (Dowsett & Dowsett-Lemaire 1993). Other akalatt species form much deeper branches which are not well supported (unpublished data).

11.45% between them. It is noteworthy that all *S. sharpei* samples (which include representative of populations collected southwest and east of the Nguu Mountains) form a very close-knit group with an average sequence divergence of only 0.9% between disjunct populations. The *S. gunningi* samples were much more dissimilar, with an average sequence divergence of 3.6% between populations. The Nguu samples differed from three other populations, all from coastal forests, by an average of 3.8%.

### Ecology

*S. gunningi alticola* was common in the Nguu Mts, both in the Gombero and Lulago Forests. It was observed, mostly single birds, on the ground and flitting between low perches in undisturbed submontane forest at 1,140–1,750 m, in areas with tangled understory vegetation, often near streams and moss-covered logs. Two fledglings were collected 23 November at 1,500 m in Gombero Forest. Besides arthropods, the birds eat berries and seeds (Keith *et al.* 1992 reported the species to be insectivorous). Although situated in a slight rainshadow, the Nguu Mts receive orographic rain and probably also some mist precipitation. While some parts of the forests are rather dry, the east slopes have evergreen forest dominated by *Albizia*, *Antiaris*, *Celtis*, *Cissus*, *Olea*, *Teclea* and *Zeyherella*, with 60% canopy cover, mainly at 25–30 m, with huge *Newtonia* trees locally, and mainly *Albizia*, *Diospyros* and *Olea* on dry ridges (Lovett & P cs 1993; Seddon *et al.* 1995). Lianas and *Piper* thickets are abundant. The adjacent lowlands are woodland, bushland and bushed grassland. The species is known mainly from lowland forests, where it can be very patchy, favouring valley bottoms with a dense canopy and dense understorey thickets formed around fallen trees. Newmark (1993) found that it was vulnerable to habitat fragmentation. There are, however, some records from heavily logged, secondary and rather dry and open sites (Dowsett-Lemaire 1989, Keith *et al.* 1992, Collar *et al.* 1994).

## Discussion

The majority of the endemic forest birds of eastern Africa (east of the Albertine Rift zone; see Hall & Moreau 1970, Stattersfield *et al.* 1998, Burgess *et al.* in press) can be classified as being either coastal or montane. They comprise independent species (probably isolated since the initial breakup of the species rich Pan-African Rainforest in the upper Miocene; Fjelds  & Lovett 1997) or representatives of more recent radiations. There are relatively few cases of vicariance within the eastern forest zone, comprising (1) speciation (and subspeciation) by isolation in different montane areas (exemplified by the *Andropadus fusciceps/nigriceps* group by Roy *et al.* 1998) and (2) a vicariance pattern with sister species inhabiting montane and coastal zones, as in *Tauraco livingstonii/fischeri*, *Pogoniolulus simplex/leucomystax*, *Phyllastrephus placidus/fischeri*, the eastern *Batis* group, *Athreptes longuemareii/neglectus*, *Serinus melanochrous/burtoni*, and in the akalats. The akalats represent a rather complex situation with *Sheppardia lowei* and *montana* (Iringa and Usambara Akalats) forming a distinctive montane clade (Jensen 1989) with a relict distribution in the Iringa highland, Ukaguru and West Usambara Mts. and *S. gunningi/sharpei*. The latter two are sister species (Fig. 1) replacing each-other in coastal and lower montane forests,

respectively. However, *S. gunningi* lives far inland in Malawi, where *S. g. bensoni* is reported from Mzuzu (Kaningia) and Viphyain to the lake-shore and on the Mulanjic and Thyola Mts in the south. Here it inhabits medium rather than high altitude forest (Dowsett-Lemaire 1989). Its very rich and warm colouration, like the closely related *S. aequatorialis* and *cyornithopsis* (Dowsett & Dowsett-Lemaire 1993), and as opposed to more greyish olive-brown upperparts and yellow (*alticola*, *sokokensis*) or buff (*gunningi*, *sharpei*) breast of the eastern populations, suggests that it may represent a relatively deep branch.

The variation in species composition between Eastern Arc mountains suggest a high level of local extinction (Fjeldså & Rabøl 1995, Cordeiro in press). The Nguu population of *S. gunningi* could be interpreted as an opportunistic colonisation in response to the disappearance of the montane *S. sharpei* from one 'inselberg'. However, the genetic distinctness of *S. gunningi alticola* suggests that it has been present here since before the differentiation of populations in *S. sharpei*. *S. gunningi* may possibly have inhabited the full range of eastern forest habitats, but was displaced from most montane forests by the successfully expanding *S. sharpei*. The internal branching in *S. sharpei* suggests that its highest genetic diversity is in the east (Usambara and Nguru samples in Fig. 1), so possibly it evolved here and then colonised other mountains. *S. gunningi alticola* could have survived as a relict population since the lower Pleistocene (see Klicka & Zink 1997 for mtDNA substitution rate).

The remaining forests in Tanzania are under severe threat from the growing human population (Lovett & Wasser 1993, Burgess & Clarke in press). Fortunately, because of difficult access, the forests of the Nguu Mts are generally in a fairly pristine state. There has been some extraction of *Khaya* and *Milicia* trees in the past, but very little logging is taking place today and the whole forest area is a Catchment Forest Reserve. The Nguu Mts are recognized as an important water catchment for eastern Maasailand. In view of the small (140 km<sup>2</sup>) and fragmented range (4 main fragments) (criterion B1 of the current World Conservation Union threatened species criteria; IUCN 1994), *S. gunningi alticola* needs to be considered Near-threatened and Conservation Dependent. The species therefore belongs in the Vulnerable category of Collar *et al.* (1994).

#### Acknowledgements

This study was supported through the Danish Centre for Tropical Biodiversity (Danish Natural Science Research Council grant 11-0390). The grant covered field-work by J. Kiure and laboratory costs and salary for M. Roy. The Natural History Museum (Tring) is thanked for specimen loans.

#### References:

- Benson, C. W. 1947. Notes on Eastern and Southern African birds. *Bull. Brit. Orn. Cl.* 67: 28–35.
- Burgess, N., Fjeldså, J. & Botterweg, R. in press. The faunal importance of the Eastern Arc Mountains in Kenya and Tanzania. *J. East Afr. Nat. Hist. Soc.*
- Burgess, N. D. & Clarke, P. in press. *The coastal forests of Eastern Africa: status, history, biodiversity and conservation*. IUCN, Gland & Cambridge.
- Collar, N. J., Crosby, M. J. & Stattersfield, A. J. 1994. *Birds to watch 2. The world list of threatened birds*. BirdLife, Cambridge, U.K.

- Cordeiro, N. in press. Preliminary analyses of the nestedness patterns of montane forest birds in the Eastern Arc Mountains. *J. East Africa Nat. Hist. Soc.*
- Dowsett-Lemaire, F. 1989. Ecological and biogeographical aspects of forest bird communities in Malawi. *Scopns* 13: 1–80.
- Dowsett, R. J. & Dowsett-Lemaire, F. 1993. *A contribution to the distribution and taxonomy of Afrotropical and Malagasy birds*. Tauraco Press, Liège, Belgium.
- Edwards, S. V., Arctander, P. & Wilson, A. C. 1991. Mitochondrial resolution of a deep branch in the genealogical tree for perching birds. *Proc. Roy. Soc. Lond. B* 243: 99–107.
- Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 79: 783–791.
- Fjeldså, J. & Lovett, J. C. 1997. Geographical patterns of phylogenetic relicts and phylogenetically subordinate species in tropical African forest biota. *Biodiver. Conserv.* 6: 325–346.
- Fjeldså, J. & Rabol, J. 1995. Variation in avian communities between isolated units of the Eastern Arc Montane Forests, Tanzania. *Gerfaut* 85: 3–18.
- Gilbert, D. G. 1992. SeqApp, A biosequence editor and application programme. Biocomputing Office, Biology Department, Indiana Univ., Blumington.
- Hackett, S. J. 1996. Molecular phylogenetics and biogeography of Tanagers in the genus *Ramphocelus* Aves. *Molec. Phyl. Evol.* 5: 368–382.
- Hall, B. P. & Moreau, R. E. 1970. *An atlas of speciation in African passerine birds*. British Museum (Natural History), London.
- IUCN. 1994. IUCN red list categories. IUCN Species Survival Commission, Gland, Switzerland.
- Jensen, F. P. 1989. A review of some genera of African chats (Aves, Muscicapidae, Erithacini). *Steenstrupia* 15: 161–175.
- Keith, S., Urban, E. K. & Fry, C. H. 1992. *The birds of Africa, Volume IV*. Academic Press, London.
- Klicka, J. & Zink, R. N. 1997. The importance of recent ice ages in speciation: a failed paradigm. *Science* 277: 1666–1669.
- Lovett, J. C. & Pöcs, T. 1993. *Assessment of the conditions of the catchment forest reserves, a botanical appraisal*. Ministry of Tourism, Natural Resources and Environment, Dar es Salaam.
- Lovett, J. C. & Wasser, S. K. 1993. *Biogeography and ecology of the rain forests of eastern Africa*. Cambridge Univ. Press.
- Newmark, W. D. 1993. Tropical forest fragmentation and the local extinction of understory birds in the East Usambara Mountains, Tanzania. *Conserv. Biol.* 5: 67–78.
- Ridgway, R. 1912. *Color standard and color nomenclature*. Published by the author, Washington, D.C.
- Roy, M. S., Arctander, P. & Fjeldså, J. 1998. Speciation and taxonomy of montane greenbuls of the genus *Andropadus* (Aves: Pycnonotidae). *Steenstrupia* 24: 51–66.
- Seddon, N., Capper, D. R., Ekström, J. M., Isherwood, I. S., Muna, R., Pole, R. G., Tarimo, E. & Timothy, J. 1995. *Final report of Project Mount Nilo '95'*: A bird conservation project to the East Usambara and Nguu Mountains, Northern Tanzania. Privately published, Cambridge.
- Seutin, G., White, B. N. & Boag, P. T. 1991. Preservation of avian blood and tissue samples for DNA analysis. *Can. J. Zool.* 69: 82–90.
- Stattersfield, A. J., Crosby, M. J., Long, A. J. & Wege, D. C. 1998. *Endemic Bird Areas of the world. Priorities for biodiversity conservation*. Birdlife, Cambridge, U.K.
- Svensson, L. 1992. *Identification guide to European Passerines*. Published by the author, Stockholm.
- Swofford, D. L. 1991. PAUP: *Phylogenetic analysis using parsimony. Version 3.1*. C. Biodiv. 111. Nat. Hist. Survey, Champaign, 111.
- Addresses:* Jon Fjeldså, Centre for Tropical Biodiversity, Zoological Museum, Universitetsparken 15, DK-2100 Copenhagen, Denmark. Michael S. Roy, Centre of Tropical Biodiversity, Zoological Institute, Universitetsparken 15, DK-2100 Copenhagen, Denmark. (Current address Department of Zoology, Ottago University, PO Box 56, Dunedin, New Zealand).
- Jacob Kiure, Consolidated Investment Ltd., PO Box 1194, Dar es Salaam, Tanzania.